A NEW GENUS OF CALCEOCRINID FROM SPAIN WITH COMMENTS ON MOSAIC EVOLUTION

by G. D. WEBSTER

ABSTRACT. *Espanocrinus lemonei* n. gen., n. sp. is the first calceocrinid crinoid reported from the Early Devonian of Spain. This genus has primitive main axil and arm structure and advanced dorsal cup features. This suggests that mosaic evolution occurred in the calceocrinids and that cup changes were most significant in Ordovician to Devonian time. Modifications of the main axil and arm were thereafter most important in some lineages.

DURING the 10th International Field Institute, sponsored by the American Geological Institute, a visit was made to the Devonian section on the west cape of the Bay of Arnao, near Aviles (Asturias), Spain. The geologic section there consists of interbedded grey limestones and red shales of Early Devonian (Emsian) age thrust over Late Carboniferous (Westphalian) clastics. The limestones, which contain abundant specimens of *Trybliocrinus flatheanus* (Geinitz 1867), are correlated by Comte (1959) to the La Vid Shale and considered to be of early Emsian age.

While studying the *T. flatheanus* beds a calceocrinid was discovered by Dr. David LeMone who generously turned the specimen over to me for further investigation. That specimen is the first known calceocrinid from Spain and adds to the known evolutionary morphology and geographic distribution of this unique group of crinoids.

The calceocrinids are a unique family of the inadunate crinoids. Their primary distinguishing features are the possession of pronounced E ray bilateral symmetry and a transverse hinge crossing the cup beneath the E inferradial. The crowns are generally slender and elongate. The E ray arm is more robust than all others. In the enclosed position the crown commonly folds down against the proximal stem. Their greatest diversity occurred in the Devonian after which they declined rapidly to a rather small segment of crinoid faunas. Calceocrinids persisted until Early Permian time.

Morphologic terms used in the accompanying description follow those proposed by Moore (1962) and Moore and Strimple (1973).

SYSTEMATIC PALAEONTOLOGY

Subclass INADUNATA Wachsmuth and Springer, 1885
Order DISPARIDA Moore and Laudon, 1943
Superfamily HOMOCRINIDAE Ubaghs, 1953
Family CALCEOCRINIDAE Meek and Worthen, 1869
Genus *Espanocrinus*, n. gen.

Diagnosis. A calceocrinid with perfect bilateral symmetry, weakly gaped hinge, adjoined large radials; three basals, DE and EA basals fused into adanally convex

[Palaeontology, Vol. 19, Part 4, 1976, pp. 681-688, pl. 103.]

triangular plate, AB and CD basals rectilinear sharing stem attachment; prominently protruded anal tube at base of crown; undivided median arm; 6 axial arms, 3 each side; 4 main axil plates, only second and fourth axillary with largest branch always abanal.

Description. See the following description of the type species and plate diagram (text-fig. 1).

Type species. E. lemonei.

Espanocrinus lemonei, n. gen., n. sp.

Plate 103; text-figs. 1–2

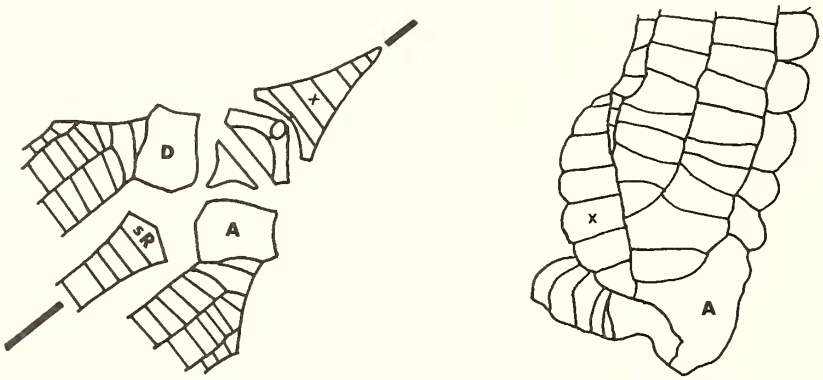
Material. One crown, to be deposited in the U.S. National Museum, Smithsonian Institution, USNM 221559.

Diagnosis. As for the genus.

Description. Crown: perfect bilateral symmetry, slender, elongate, gently curved adanal distally; length 80·5 mm curved, 87·7 mm along curvature, most distal brachial lacking; width at hinge slightly incomplete 12·4 mm, at large radials 12·0 mm, at IBr_{10} of median ray 8·2 mm, at distal tip 4·4 mm; depth at maximum through IBr_1 of median ray to tp_3 14·7 mm, at IBr_{10} of median ray 10·7 mm, at distal tip 3·6 mm.

Cup: higher than wide in median ray view, sharply constricted above hinge on sides of large radials, tapers moderately toward median ray on distal tip of large radial and across lateral edges of superradial of median ray; triangular in basal view, greatest dimension along hinge line; maximum height 12·2 mm, maximum width through large radials 12·0 mm; in enclosed position basal surface makes a right angle with base of median ray surface.

Basals: three; EA–DE basals fused into a single convex subtriangular plate, straight along hinge line, 7·5 mm long, convex adanally, 4·0 mm wide, slightly more triangular appearing than crescent-shaped in outline; AB and CD basals mirror images, both appear somewhat dumb-bell-shaped, larger on the ends and constricted



TEXT-FIG. 1. *Left*, plate diagram of *Espanocrinus*, n. gen., diagrammatic, based on holotype. Plane of symmetry indicated by heavy diagonal line; X, primanal; A and D, radials; sR, E ray superradial. *Right*, *E. lemonei*, n. gen., n. sp., right anterior view of holotype, taken from inked bleached photograph (×2).

in the centre, concave exterior, adjoin large radial abanally, enclose DE–EA basal adanally, mutually share stem attachment, maximum width 9·0 mm, height at stem attachment 3·9 mm, at central constriction 2·7 mm, at slightly incomplete hinge end 4·5 mm. In retracted position the AB and CD basals touch against the A radial–B inferradial and D radial–C inferradial respectively; in expanded position B and C radials would not be in contact with AB and CD basals respectively.

Radials: large A (anterior) and D (left posterior) radials mirror images, sideways V-shaped in median ray view caused by constriction between hinge bulge at base and outflaring of distal two-fifths of plate with gently inward bending of distal tip, constriction sharp enough to appear as a suture on sides of cup but not on the median ray side, A radial bounded in a clockwise direction by E superradial, D radial, E inferradial, AD basal, B inferradial, IBr_1, and IBr_2; height 9·8 mm, width 7·2 mm, A and D radials mutual suture 2·1 mm long; small inverted T-shaped E inferradial with concave sides where adjoined to radials, hinge slightly deformed, height 4·8 mm, width 8·2 mm, A and D mutual suture 2·1 mm; E superradial convex proximally and adanally, moderately inflated transversely on exterior, moderately concave distal surface, width at base 9·6 mm, width at top 8·0 mm, midheight 3·0 mm, slight proximal flare on proximal lateral edge; B and C inferradials triangular in outline, partly covered by proximal stem segments, possibly but doubtfully fused into one plate, probably have a mutual groove or impression that the proximal three or four stem segments fit into when crown is in the enclosed position, concave distal surfaces; subanal (B–C superradial) one fused plate, moderately convex proximal surface, gently concave distal surface, strongly protruded exterior surface, twice as wide as high; primanal immediately above subanal and of same protruding shape, slightly distorted in preservation, followed by four tube plates each decreasing in size to the small half-conical pointed fourth one, all strongly protruded exteriorly.

Arms: seven, elongate, unbranched. E ray brachials wider than high, strongly bulbous but more so transversely than laterally, slight flange along lateral edges with adjoining arms, IBr_1 9·0 mm wide, 3·0 mm high; IBr_2 7·0 mm wide, 3·9 mm high; IBr_{10} 6·6 mm wide, 3·7 mm high; IBr_{20} 4·5 mm wide, 3·3 mm high. Main axils four in each lateral ray only two of which in each ray are axillary; main axil I non-axillary, wedge-shaped pointed abanally, convex proximal surface, planar distal surface; main axil II axillary, wider branch abanally, approximately twice as wide as high, planar proximal surface, gently concave branching surfaces; main axil III non-axillary, wedge-shaped, pointed abanally, gently convex proximal and distal surfaces, approximately two-fifths as high as wide; main axil IV axillary, much wider branch abanally, gently concave proximal surface and moderately convex distal surface. Six lateral or axil arms, three each side, unbranched thus each composed only of alpha brachial, largest abanal, central one only slightly smaller than abanal one, adanal ones (omega) markedly smaller not reaching apex of crown, left posterior omega arm two-thirds shorter than A ray omega arm; centrally elevated ridge extending length of arms, producing a ribbed appearance to the crown, faint flange on lateral edges of brachials.

Stem round, axial canal round, column tapers distally; proximal five columnals preserved; diameter of proximal columnal 4·7 mm, diameter of fifth columnal 4·1 mm.

Remarks. The symmetry and cup structure of *Espanocrinus lemonei* show advanced evolutionary features of the Calceocrinidae. That is, the symmetry is perfectly bilateral, the A and D radials are adjoined separating the E inferradial and superradial, the DE and EA basals are fused into one plate, the B and C inferradials are in contact, and the stem is moved back, attaching on to the AB and CD basals only. All these features are found also in *Halysiocrinus*. The structure of the main axils is primitive in that there is a non-axillary main axil below each axil; this is common in *Calceocrinus*, *Cremacrinus*, and *Anulocrinus*, the three oldest known genera of the family. In addition, the lack of branching on the median and axil arms is considered primitive, as is the small number of arms. Thus, both advanced and primitive features are found on *Espanocrinus*, as might be expected of a calceocrinid occurring near the midrange (Early Devonian) of the time span of the family (Middle Ordovician–Early Permian).

A comparison between *Espanocrinus* and previously described calceocrinid genera strongly suggests that mosaic evolution took place in the calceocrinids. It clearly shows that, at the generic level, different parts of the crown were evolving at different rates. Evolution of the cup was exceedingly important in the Ordovician, Silurian, and Early Devonian, as pointed out by Kesling and Sigler (1969). In Middle Devonian to Permian time, changes were still occurring in the cup but they appear to be less significant than changes in the main axils, anal tube, and arms. Thus advanced configuration of the cup plates preceded modifications in the main axils and arms. This is undoubtedly related to the function of the animal and may reflect a modification in feeding habit or environment.

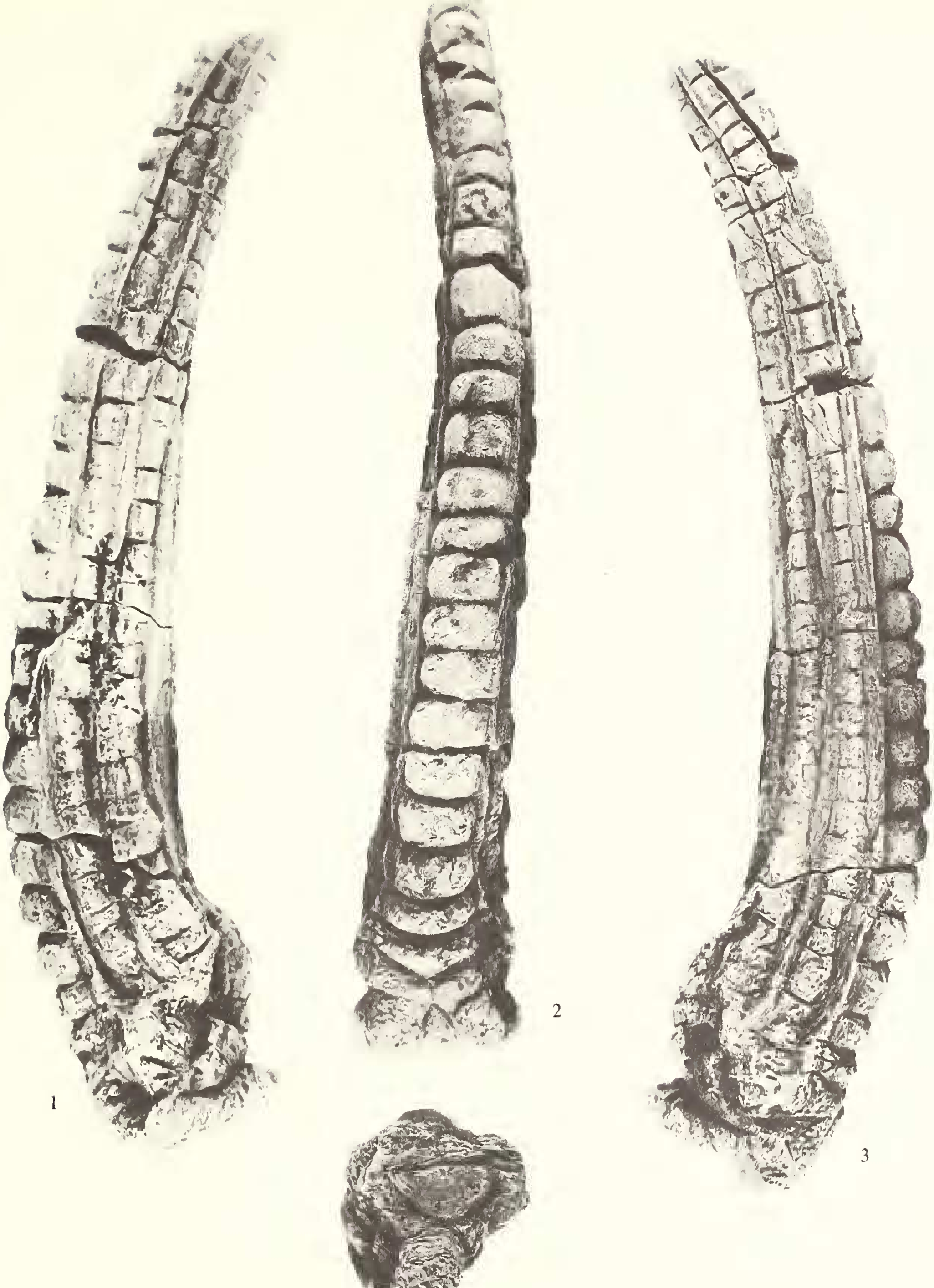
Two genera of calceocrinids, *Eohalysiocrinus* and *Halysiocrinus*, are closely allied to *Espanocrinus* in the structure of the cup. *Eohalysiocrinus* is a small form in which the main axils are not developed, and the C and B inferradials are very short (Prokop 1970). This contrasts with the poor to moderate development of the main axils and longer C and B inferradials on *Espanocrinus*. The position of the columnar facet is shared on the AB and CD basals, tangent to the third basal, in *Espanocrinus*; in *Eohalysiocrinus* the same condition may exist or the stem facet may be shared by all three basals. *Halysiocrinus* differs in having highly developed main axils and the stem facet restricted to the AB and CD basals.

Because the cup plate arrangement of *Espanocrinus* is so similar to that of *Halysiocrinus*, a careful review of the species assigned to the latter genus was made. This review of the thirteen species assigned to *Halysiocrinus* by Moore (1962) and Brower (1966) revealed that three are of Middle Devonian age and ten are of Early Mississippian age.

The three Middle Devonian species have strongly protruding anal tubes at the base of the crown, as in *Espanocrinus*, but seven to ten branching axil arms on each side of the cup, whereas *Espanocrinus* has only three unbranching axil arms. I believe that these three forms represent a new genus of calceocrinid.

EXPLANATION OF PLATE 103

Figs. 1–4. Holotype of *Espanocrinus lemonei*, n. gen., n. sp. 1, left posterior view; 2, median view; 3, right anterior view; 4, basal view. All views ×2.



WEBSTER, Calceocrinid from Spain

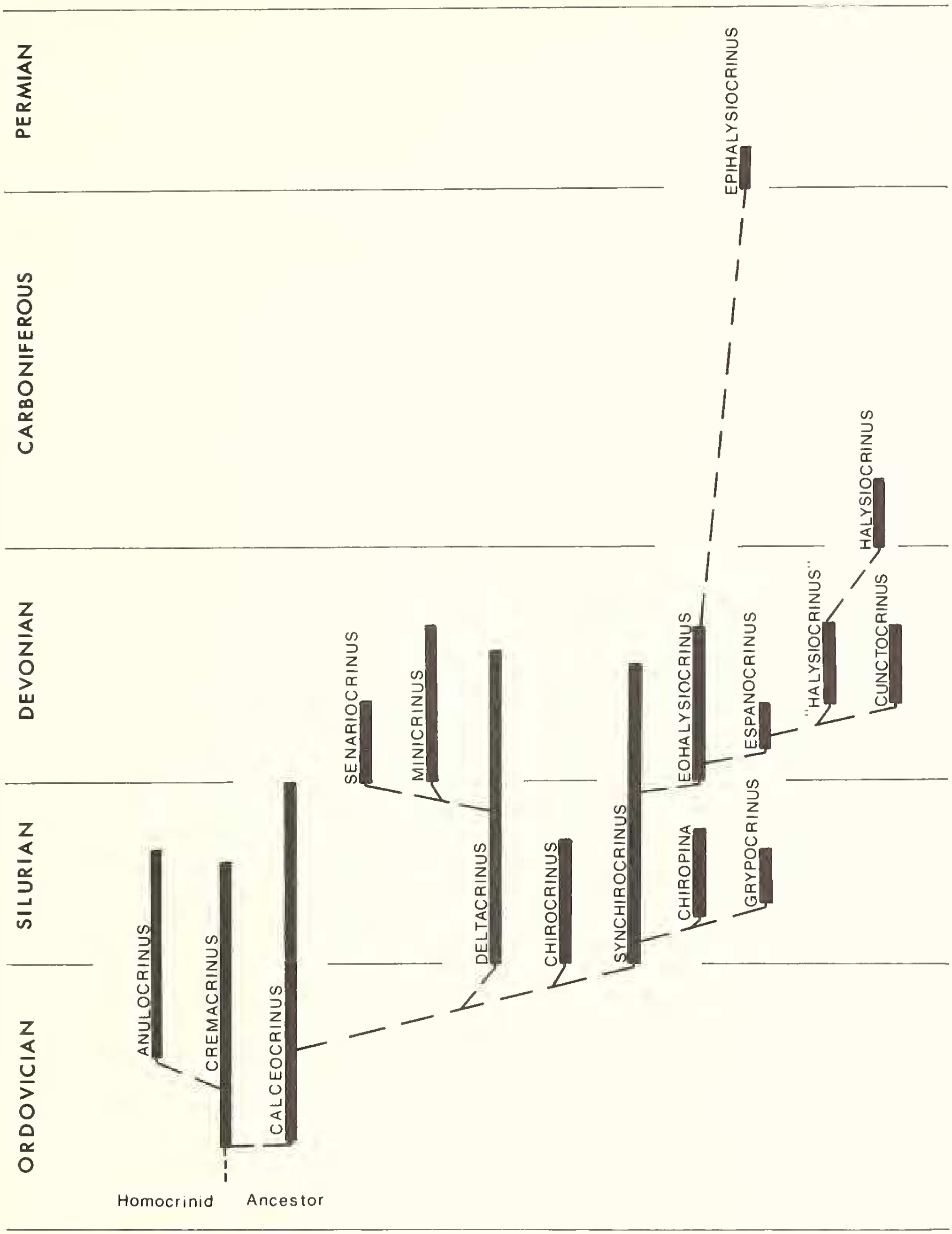
The ten Early Mississippian species assigned to *Halysiocrinus* include the type species *H. dactylus* Hall, 1860, and also *H.*? *lamellosus* (Hall, 1860), a *nomen nudum* based on an undescribed, unillustrated set of arms. The remaining nine species show two cup shapes. One is relatively elongate, high enough to have a gap between the column and the main axils when the cup is enclosed and the hinge forms a right angle in the enclosed position. The second has a relatively low cup, and in the enclosed position the column is against the main axils and the hinge forms an acute angle. In addition, the Mississippian species of *Halysiocrinus* lack, or have a very small, protruding anal tube at the base of the crown, and the arms enshroud the anal tube. They generally have four or five branching axil arms—the reported acutal range is three (*H. bradleyi* (Meek and Worthen, 1860)) to seven (*H. nodosus* (Hall, 1860) has from five to seven axil arms). I consider both *H. nodosus* and *H. robustus* (Worthen, 1890) to be junior synonyms of *H. tunicatus* (Hall, 1860).

Thus Mississippian species of *Halysiocrinus* have more axil arms than *Espanocrinus* but generally fewer than Devonian species of *Halysiocrinus*, and they lack the prominent anal tube found in *Espanocrinus* and the Devonian forms. In addition, *Espanocrinus* has one non-axillary main axil below each axillary (text-fig. 2). Only two species of the Devonian and Mississippian halysiocrinids have non-axillary main axils; these are *H. elephantinus* Laudon, 1936 (Devonian) which has only main axil I_1 non-axillary, whereas *H. springeri* Brower, 1966 (Mississippian) has main axil I_1 and II_1 non-axillary but no others.

In all calceocrinids, except *Espanocrinus*, the adanal is the longest of the branching sutures of any axillary main axil, and the abanal is the shortest, except that the reverse condition is found in the last or omega ramule branch. In *Espanocrinus* the longest suture is always the abanal one.

Brower (1966) suggested that *Halysiocrinus* was possibly derived from *Deltacrinus*, pointing out the similarity of arm branching and separation of the E ray inferradials and superradials. Moore (1962) interpreted *Deltacrinus* and *Halysiocrinus* as descendants of *Calceocrinus*. However, he believed that the Ordovician to Early Devonian forerunners of *Halysiocrinus* were unknown. *Espanocrinus* fills the Early Devonian gap in this lineage. It is not thought to have evolved from *Deltacrinus*, because of the moderate development of the unbranched main axils. The three Middle Devonian species of *Halysiocrinus* were probably derived from *Espanocrinus* and in turn gave rise to the Early Mississippian halysiocrinid species.

The phylogeny of the calceocrinids has been discussed by several authors recently. Prokop (1970, fig. 19) followed the phylogeny of Moore (1962, fig. 21) with slight modifications. Kesling and Sigler (1969, fig. 10) and Rowell (1969, fig. 2) approached the phylogeny from two numerical taxonomic methods that resulted in moderately similar phylogenies which differ significantly from that of Moore (1962). Some difficulties are noted in these phylogenies when time is considered. Rowell (1969) shows *Chirocrinus* (Early–Middle Silurian) and *Synchirocrinus* (Early Silurian–Middle Devonian) as derived from *Grypocrinus* (Middle Silurian). Kesling and Sigler (1969) and Rowell (1969) show *Seniocrinus* (Early Devonian) derived through *Cunctocrinus* (Middle Devonian) from *Halysiocrinus* (Middle Devonian–Early Mississippian). Rowell (1969, p. 232) noted that the spacing in his fig. 2 for *Senariocrinus* was equidistant from *Deltacrinus* (Early Silurian–Middle Devonian) and



TEXT-FIG. 2. Stratigraphic distribution and inferred phylogenetic relationships of the genera of the Calceocrinidae.